NEST AND DUCKLING SURVIVAL OF SCAUP AT MINTO FLATS, ALASKA

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A

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Abstract: To address the hypothesis that declines in recruitment were related to recent declines in abundance of lesser and greater scaup, I estimated variation in nest and duckling survival of these species at Minto Flats, Alaska (64°50′N, 148°50′W) during 2002-2003. I included nest survival data from two previous studies conducted during 1989-1993 in my analysis. Daily Survival Rate (DSR) of nests was variable within and among years and among habitats. Estimated nest survival of scaup ranged from 0.02 (95% CI: 0.00 to 0.06) in 1992 to 0.61 (95% CI: 0.50 to 0.74) in 1993. Predation was the primary apparent cause of nest failure, and flooding of nests was an important secondary influence. DSR of ducklings varied between years and increased with age of the ducklings and body condition of the brood female. Duckling survival to 30 days was: 0.24 (95% CI: 0.16 to 0.36) in 2002 and 0.03 (95% CI: 0.00 to 0.19) in 2003. I conclude that high temporal variability in production of scaup at Minto Flats was likely related to annual variation in the risks of predation and flooding and indicated that intermittent years of high production could be particularly influential to this population.

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PREFACE

The body of my thesis comprises two manuscripts prepared for joint submission to the Journal of Wildlife Management. I collected data on nest and duckling survival during 2002-2003 and supplemented my analysis of nest survival with data collected by previous investigators during 1989-1993. Although both manuscripts have coauthors listed, I was responsible for the analysis, interpretation, and reporting of these data, as well as data collection during 2002-2003. Thus, I take full responsibility for any errors in this work. The "we" contained in these manuscripts refers to me, my coauthors, and the field technicians who assisted with data collection.

This project would not have been possible without the financial, logistical, and technical support of several organizations and numerous individuals. Financial support was provided by Ducks Unlimited's Institute for Wetland and Waterfowl Research, The Institute of Arctic Biology and Department of Biology and Wildlife at the University of Alaska Fairbanks, The Sally M. and Edward D. Futch Graduate Fellowship, The Ted McHenry Biology Field Research Fund, and The University of Alaska Fairbanks Thesis Completion Fellowship. I received logistical support from the Institute of Arctic Biology, United States Fish and Wildlife Service, The Alaska Cooperative Fish and Wildlife Research Unit, and The Alaska Department of Fish and Game. Marta Conner, Ed Debevec, Wanda Fields, Jason Jack, and Genelle Tilton of the Institute of Arctic Biology were especially helpful. Michelle Das, Theresa Tanner, and Kathy Pearse of the Alaska Cooperative Wildlife Research Unit patiently and competently assisted with

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My academic experience was enhanced considerably by the quality of my advisors and fellow students. My major advisor, Mark Lindberg, has generously shared his knowledge and experience with me for the past five years. His influence on me is indelible; I will never be irresolute about the need for scientific rigor in wildlife management. My advisory committee members, Abby Powell and Eric Rexstad, have been consistently helpful in all matters related to this project. They raised many useful points at every stage of my project, and contributed greatly to my development. Eric also provided hand-held computers that were particularly helpful for data collection. Fellow graduate students John Citta, Steve Hoekman, Bryce Lake, Dave Safine, and Josh Schmidt regularly discussed this project with me. Those discussions were critical to my thinking and the quality of my work. Finally, thanks to Bryce Lake for helping me to create readable maps of my study area

INTRODUCTION

The abundance of wildlife populations is rarely constant across space and time. Imbalance between processes of addition (births, immigration) and reduction (deaths, emigration) acts to produce natural variability in population size (Gotelli 1998). Understanding the patterns and mechanisms of variation in abundance is of major interest to ecologists and wildlife managers who seek to conserve wildlife populations. For example, information about sources of variation in abundance is fundamental to the effective management of North American waterfowl species exposed to annual sport harvest (US Fish and Wildlife Service 2003*a*).

Knowledge of abundance alone, however, will not allow the observer to distinguish among the sources of variation responsible for population fluctuations. That is, in a series of abundance estimates the effects of immigration and emigration on population dynamics are indistinguishable, respectively, from the effects of birth and death, and any of these processes is a synthesis of multiple parameters; each influenced by a suite of ecological and environmental factors (Johnson et al.1992, Gotelli 1998). Moreover, abundance can seldom be enumerated exactly; rather, it must be estimated from sample data. Thus, series of abundance estimates represent population dynamics at the coarsest scale, combined with the additional uncertainty of sampling variance (Link and Nichols 1994). The limitations of these data notwithstanding, such information can reveal extensive patterns of population dynamics that are of interest to wildlife managers, and indicate worthwhile directions for more intensive studies of demographic rates.

Annual estimates of spring abundance for several species of North American ducks are available from the mid-1950s to the present (US Fish and Wildlife Service 2003*b*). These estimates are obtained through aerial surveys across the entire breeding range, and therefore avoid most confusion between movement and absolute increases and decreases in abundance. They may include some bias within years due to timing of survey flights relative to patterns of migration (Naugle et al. 2000), and imperfect detection (Austin et al. 1998), but errors are inconsistent among years. Thus, distinct and consistent temporal patterns in spring abundance estimates most likely reflect changes in recruitment (i.e., birth) and mortality (i.e., death) rates, or both (Afton and Anderson 2001, Koons and Rotella 2003). For instance, past trends in the abundance of mallards (*Anas platyrynchos*) and many other populations of North American duck species, especially dabbling ducks (*Anas* spp.), have been strongly related to environmental factors on mid-continent breeding areas. Mallard recruitment has increased and decreased concurrent with wet and dry conditions in the Prairie Pothole Region and Canadian prairie-parklands, producing corresponding variation in overall mallard abundance (US Fish and Wildlife Service 2003*a*). Managers of mid-continent mallards have traditionally accounted for current wetland conditions in these regions when setting subsequent fall hunting seasons and bag limits, as well as when defining habitat conservation goals. Nevertheless, those species that do not predictably increase and decrease in abundance with the cycles of drought and precipitation in mid-continent

breeding regions require different research priorities and management prescriptions than mallards.

An ongoing (25-year) decline in the abundance (mean annual decline ± SE: 150,491 ± 25,100) of the combined spring population of lesser (*Aythya affinis*) and greater (*A. marila*) scaup has generated considerable scientific and management concern (United States Fish and Wildlife Service 1999, Austin et al. 2000, Afton and Anderson 2001). The combined population of scaup has not exceeded its long-term average of 5.3 million individuals since 1986, and while mallard abundance increased in response to improved habitat conditions in the mid-continent during the 1990s, scaup populations continued to decline (Wilkins and Otto 2003). Scaup are still the most abundant diving ducks in North America; however, the estimated 2003 breeding population of 3.7 million (US Fish and Wildlife Service 2003*b*) was considerably below the goal of 6.3 million set by the North American Waterfowl Management Plan (US Fish and Wildlife Service and Canadian Wildlife Service 1986, US Fish and Wildlife Service 2003*a*). Furthermore, abundance of scaup has not declined uniformly throughout the breeding range (Afton and Anderson 2001). Scaup populations in the boreal forest west of the continental divide, and in tundra regions, appear to have been stable or declined less severely than those in the boreal forest east of the divide. The majority of scaup breeding in tundra areas (e.g., the Yukon-Kuskokwim Delta of Alaska) are greater scaup (Kessel et al. 2002). These observations indicated that spatial, interspecific, and temporal variation in demographic rates might have influenced scaup abundance at regional and continental scales.

Afton and Anderson (2001) performed a retrospective analysis of data from harvest surveys (1978 –1997) and observed evidence of an increasing ratio of males to females and a decreasing ratio of juveniles to adults in the harvest of lesser scaup. They observed that population size was unrelated to harvest rate during the same period; thus, they concluded that reduced recruitment, rather than over-harvest, was the most likely mechanism of the decline in lesser scaup abundance.

Little quantitative information is available to accurately describe the reproductive ecology of either species of scaup or other duck species in the boreal forest region. Because the majority (68%) of North American lesser scaup breed in the boreal forest, information from this region is vital to any assessment of trends in the population (Austin et al 1998, Austin et al. 2000, Afton and Anderson 2001). Intensive studies of the reproductive success of both species of scaup across their entire breeding range were recommended by Austin et al. (2000) and Afton and Anderson (2001) to provide information for the management of declining scaup populations.

I initiated a two-year study of scaup reproductive success at Minto Flats State Game Refuge (64°50' N, 148°50' W), 35 km north west of Fairbanks, Alaska, in May 2002. Ecological research on waterfowl production conducted intermittently since the 1950s (Hooper 1952, Rowinski 1958, Mann 1993, Petrula 1994, MacCluskie 1997) and abundance estimates from US Fish and Wildlife Service spring population surveys (Conant and Hodges 1985) indicated that the predator community, habitat types, and the breeding waterfowl community at Minto Flats were typical of the western boreal forest. I

also anticipated adequate data to compare reproductive success of greater and lesser scaup in sympatry. For these reasons I expected that a study of scaup production at Minto Flats would not only be feasible, but useful.

My primary goal was to estimate nest and duckling survival of lesser and greater scaup at Minto Flats and to describe patterns of variation in these parameters relative to environmental and ecological factors of interest to waterfowl managers. More specifically, I was interested in variation in nest survival of both species of scaup during our study relative to characteristics of the nest site (e.g., habitat type, distance from water), timing of nesting, and other species of ducks nesting on the study area. I was further availed of nest survival data for all species of ducks nesting at Minto Flats during 1989-1993 through cooperation with previous researchers (Petrula 1994, MacCluskie 1997). Therefore, my objectives also included estimation of annual variation in nest survival during 1989-1993 as well as 2002-2003 (Chapter 1). I sought to relate variation in duckling survival to attributes of the brood female, environmental conditions, year, timing of hatch, and age of the ducklings. I wanted additionally to use estimates of nest and duckling survival generated by my research effort to estimate recruitment (i.e., the number of female ducklings surviving to fledge), and to develop preliminary models of scaup production at Minto Flats (Chapter 2). I designed the research and modeling efforts to ensure that results would be comparable to past studies at Minto Flats, as well as to concurrent studies of the reproductive success of scaup at other sites in the boreal forest of Alaska and Canada.

NEST SURVIVAL OF SCAUP AT MINTO FLATS, ALASKA[1]

Abstract: We estimated variation in nest survival of lesser (*Aythya affinis*) and greater (*A. marila*) scaup and other common duck species at Minto Flats, Alaska during 1989-1993 and 2002-2003. Nest survival of scaup, as well as all other species, varied with year, date, and nest habitat. Species, nest age, and distance to water were less useful predictors of nest survival. Average annual nest survival of all ducks at Minto Flats was 0.11 (95% CI: 0.05 to 0.22) comparable to nest survival of ducks breeding in mid-continent regions (e.g., the prairie pothole region and the Canadian prairie-parklands). Nest survival of scaup was highly variable among years ranging from 0.01 (95% CI: 0.00 to 0.06) in 1992 to 0.61 (95% CI: 0.50 to 0.74) in 1993, and was probably related to variation in predation and water levels. Scaup production could have been limited by low nest survival during most years of this study; nest survival exceeded 20% only in 1993 and 2002. Because of the demonstrated importance of Minto Flats to breeding scaup and

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other waterfowl, we recommend management to maintain existing habitat for scaup and other duck species. This management could be most effectively informed by monitoring of annual production to more accurately understand spatial and temporal variation in recruitment of scaup, and identify potential effects of proposed oil and gas exploration on recruitment of ducks at Minto Flats.

Key words: Alaska, *Aythya affinis*, *Aythya marila*, boreal forest, ducks, nest success, nest survival, population dynamics, scaup.

INTRODUCTION

Changes in the overall abundance of wildlife populations through time are brought about by changes in reproduction and survival rates (Gotelli 1998). When managed species exhibit temporal trends in abundance, wildlife managers and ecologists seek to discern the demographic source of these trends in order to guide management decisions (Johnson and Shaffer 1987, Austin et al. 2000, Wilkins and Otto 2003).

The total abundance of the North American populations of lesser and greater scaup has declined at the annual rate of 150,491 (SE = 25,100) individuals/year since 1978 (Austin et al 2000, Afton and Anderson 2001). This decline has been temporally consistent, but regionally variable. Abundance of scaup has declined most in the boreal forest of Canada east of the continental divide. In the boreal forest of Alaska and Canada west of the continental divide, as well as in tundra regions of Alaska and Canada, scaup abundance has declined less severely or remained stable during the past 25 years (Afton

and Anderson 2001). Because most of the scaup in tundra regions are greater scaup (Kessel et al. 2002), some researchers have speculated that the decline in scaup abundance has been more directly related to declines in lesser scaup abundance (Afton and Anderson 2001, Koons and Rotella 2003). These patterns have revealed a need for demographic information about both species of scaup where they occur in sympatry and from sites throughout the boreal forest to distinguish geographic (e.g., environmental) from interspecific variation in demographic rates.

Concerned waterfowl ecologists, citing concurrent declines in the ratio of juvenile to adult lesser scaup in the fall sport harvest, have hypothesized that the decline in abundance of scaup in North America could have been caused by regional declines in recruitment of juvenile lesser scaup to the fall population (Austin et al. 2000, Afton and Anderson 2001). Recruitment to the fall population in ducks is defined as the product of breeding probability, breeding season survival of females, clutch size, egg survival, re-nesting rate, nest survival, and duckling survival (Johnson et al. 1992). These components of recruitment have not been thoroughly described for either species of scaup in its primary breeding range, however (Austin et al. 1998, Kessel et al. 2002). In fact, with some exceptions, (Petrula 1994, Grand 1995, Fournier and Hines 2001) little recent research effort has been directed toward recruitment of ducks in the boreal forest, where the majority of North American lesser scaup spend the breeding season and scaup abundance has declined most (Austin et al. 1998).

Nest survival, the probability that a nesting attempt results in ≥1 egg hatching, has been identified as one of the most influential components of recruitment, and ultimately the rate of population change (λ), for some duck species. Nest survival and hen success (i.e., nest survival rate * re-nesting rate) are the most influential parameters in models of the reproductive success of mallards (Cowardin et al. 1985, Johnson et al. 1992). Changes in nest survival have a greater effect on the population dynamics of mid-continent mallards than proportional changes in any other parameter in the annual cycle; including survival of females during the non-breeding season (Hoekman et al. 2002). Hen success strongly influences the local dynamics of canvasback (*Aythya valisineria*) populations in Manitoba (Anderson et al. 1997, Anderson et al. 2001) and nest survival has considerable effect on local population dynamics of lesser scaup in the boreal forest of Northwest Territories (Brook 2002) and the parklands of Manitoba (Koons 2001, Koons and Rotella 2003).

Moreover, methods for studying nest survival of ducks are highly standardized (Klett et al. 1986). Therefore, we studied nest survival of scaup and other ducks at Minto Flats because nest survival has been influential to recruitment in these species (Koons 2001, Brook 2002), and comparable nest survival data can be collected at widely dispersed study areas.

We studied nest and duckling survival of scaup during 2002-2003 at Minto Flats State Game Refuge in the boreal forest of interior Alaska. We examined variation in nest survival of both species of scaup and several other duck species relative to characteristics

of nest sites (e.g., nest habitat, distance from water), age of the nest, timing of nesting, and other species of ducks nesting on the study area. We were further provided, through cooperation with previous investigators (Petrula 1994, MacCluskie 1997), with comparable nest survival data for all species of ducks, including greater and lesser scaup, that nested at Minto Flats during 1989-1993. Therefore, we expanded our objectives to include estimation of annual process variation in nest survival during 1989-1993 and 2002-2003.

Guided by the results of previous research, we developed predictions about the relationship that each measured covariate was likely to have with nest survival. Because predation has been the primary apparent cause of nest failure for ducks (Johnson et al. 1992, Sargeant and Raveling 1992, Greenwood et al. 1995) our predictions were cast in terms of predation risk. We also included some discussion of vulnerability to flooding, an important secondary cause of nest failure at Minto Flats (Petrula 1994, MacCluskie 1997).

Nest survival of ducks can vary among habitat types, as nests located in some habitat types—on islands, for example—might be less vulnerable to mammalian predators (Lokemoen 1991, Lokemoen and Woodward 1992). Also, we predicted that nest survival was likely to increase linearly with distance from water; as nests located farther from water could be less vulnerable to both predators (Kantrud 1993) and flooding (Petrula 1994).

Seasonal trends in nest survival could be related to the abundance of alternative prey available to nest predators, phenology of nesting cover (Grand 1995, Johnson et al. 1992), and, at Minto Flats, changes in water levels (Petrula 1994, Larsen 1997). Such potential influences indicated to us that trends in nest survival throughout the nesting season could be more likely than a constant daily survival rate (Klett and Johnson 1982). We predicted that nest survival would increase with nest initiation date, because abundance of alternative prey was likely to increase through the season (Grand 1995, Greenwood et al.1995) and most flooding at Minto Flats occurs early in the season (Petrula 1994). We further predicted that date effects on nest survival might manifest as quadratic relationships if availability of alternative prey began to decline after reaching a seasonal peak, patterns of predator activity changed within the season, or melting of ice pavements (Petrula 1994) caused late-season flooding of nests in floating vegetation habitat.

Nest survival also could be expected to increase with nest age, as nests located at highly vulnerable points (e.g., near a travel route used by predators of nests) are more likely to be destroyed at an early age (Klett and Johnson 1982, Johnson et al. 1992, Dinsmore et al. 2002). Additionally, effects of nest age could be related to age and experience of the nesting female (Trauger 1971, Afton 1984) or other unspecified within-season variation among nests not explained by other variables (Nartarjan and McCullogh 1999). Consequently, we predicted increasing nest survival with nest age.

Nest survival rate could be a salient characteristic of different species or tribes of ducks. Average nest initiation date, habitat use, and nesting behavior (e.g., nest abandonment rate) are characteristics that vary among species of ducks, and could lead to characteristic nest survival rates (Johnson et al. 1992). A more parsimonious description of this variation could be obtained if these qualities varied systematically between tribes of ducks. For example, scaup and other diving ducks (*Aythya* spp.) tend to nest later, closer to water, and may have lower nest attentiveness (Austin et al. 1998, Kessel et al. 2002) than mallards or other dabbling ducks (*Anas* spp.; Bellrose 1980). Furthermore, information about the nest survival of both species of scaup, as well as other common species nesting on the study area, could indicate whether scaup, and lesser scaup in particular, have inherently lower nest survival than other species (Koons and Rotella 2003).

Among-year fluctuations in nest survival may be due to fluctuations in predator distribution and abundance (Sargeant and Raveling 1992), changes in quality and quantity of nesting habitat, and stochastic events, such as storms and floods (Johnson et al. 1992). The boreal forest, however, is generally considered to be relatively stable, in terms of habitat availability and predator community composition, when compared to mid-continent regions because of its remoteness (Jessen 1981, Johnson and Grier 1988, Rohwer 1992, Sargeant and Raveling 1992). Previous studies demonstrate, however, that rates of nest predation are similar between the boreal forest and the mid-continent (Petrula 1994, Grand 1995). Therefore, we predicted similar average values of nest

survival, but less variation in nest survival among years at Minto Flats when compared to nest survival of ducks in the mid-continent.

STUDY AREA

Minto Flats State Game Refuge (64°50′N, 148°50′W) is located in the boreal forest of interior Alaska, approximately 55 km north west of Fairbanks and 220 km south of the Arctic Circle (Fig. 1). The refuge includes 145,000 ha of forests and rivers interspersed with semi-permanent wetlands and eutrophic lakes (Jacobs 1992, Petrula 1994, Larsen 1997).

Climate at Minto Flats is best described as continental sub-arctic, with high seasonal variation in photoperiod and temperature as well as low annual precipitation (range: 18-43cm; Rowinski 1958, Petrula 1994). The Minto Flats watershed is drained by the Chatanika, Tatalina, and Tolovana Rivers, and Goldstream Creek (Petrula 1994), has little topographic relief (<15 m; Rowinski 1958, Petrula 1994), and is subject to large fluctuations of water depth within and among seasons (Rowinski 1958, Petrula 1994).

Nesting habitat for ducks at Minto Flats was composed of low-lying meadows, forested uplands, grass-shrub thickets, mats of floating vegetation, and islands. The most common plant species in meadows were bluejoint grass (*Clamagrostis canadensis*), manna grass (*Glyceria* spp.), and, in wetter areas, sedges (*Carex* spp.). Forested uplands were dominated by birch (*Betula papyrifera*) with an understory of wild rose (*Rosa* spp.), or spruce (*Picea* spp.) with dwarf birch (*Betula nana*) and Labrador tea (*Ledum decumbens*) understory. Floating mats were generally composed of buckbean

(*Menyanthes trifoliata*) and water parsnip (*Sium suave*). Grass-shrub thickets were dominated by willow (*Salix* spp.) and alder (*Alnus spp.*) with bluejoint grass in the understory. Islands were generally characterized by similar vegetation as floating mats and meadows. Larsen (1997), and Petrula (1994) provide a comprehensive description of vegetation communities and nesting habitat at Minto Flats.

During the nesting season, Minto Flats hosts a diverse group of waterfowl species in addition to greater and lesser scaup. Trumpeter swans (*Cygnus buccinator*) and white-fronted geese (*Anser albifrons*) as well as many common North American duck species, e.g., mallards and American wigeon (*Anas americana*), nest at Minto Flats. Previous research indicates that both species of scaup comprise approximately 40% of the breeding duck community at Minto Flats (Hooper 1952, Rowinski 1958, Petrula 1994). Spring surveys further reveal that the density of breeding scaup at Minto Flats has been among the highest in North America (Conant and Hodges 1985, Hodges et al. 1996).

Many species of duck nest predators (Bellrose 1980, Sargeant and Raveling 1992) occur at Minto Flats (Alaska Department of Fish and Game 1992, Petrula 1994). Avian nest predators include common ravens (*Corvus corax*), mew gulls (*Larus canus*), and herring gulls (*L. argentatus*). Mammalian nest predators, particularly red fox (*Vulpes vulpes*) and mink (*Mustela vison*), also occur at Minto Flats (Rowinski 1958, Petrula 1994).

We conducted our investigation of nest survival in an approximately 30 square kilometer area immediately surrounding Big and Little Minto Lakes (Fig. 1). This area

has been associated with the highest spring densities of ducks at Minto Flats (Rowinski 1958, Conant and Hodges 1985, Petrula 1994) and was the primary site of previous research on duck production. This study site corresponded to the core area searched by Petrula (1994) and MacCluskie (1997) and encompassed the area studied by Hooper (1952) and Rowinski (1958); thus use of this area facilitated valid comparisons between our efforts and past research.

METHODS

Data Collection

We searched for nests daily from the third week of May until the second week of July 2002-2003. We systematically rotated through various locations on the study site such that each was searched three or more times per season (every 7-15 days). All of the areas that we searched were defined by the shoreline of adjacent lakes, ponds, and channels (Fig. 1; Petrula 1994). Our objective was to search as much of the available habitat on the study site as possible, obtaining a representative sample of nests across search occasions and locations. We systematically searched meadows and islands by dragging a 30-m rope through the cover to flush the female from the nest. When dense shrubs or trees prevented us from using the rope, we walked over the entire area, using sticks and loud conversation to create as much disturbance as possible (Petrula 1994). Trained dogs also assisted with nest searching and found many nests when the female was not present.

We assigned each nest a unique number, recorded its latitude and longitude using a handheld global positioning systems receiver, and marked its location with 15-30 cm of flagging tape placed 5 m north. Using handheld computers, we recorded several variables describing the nest: species of duck, date, number of eggs, stage of incubation, habitat type, and distance from the nest to the nearest open water. If the attending female was identified as a scaup, we further numbered each egg with a permanent marker, and recorded its length and width using dial calipers ($\pm$ 0.1 mm).

We determined species by identifying the female as she flushed or, if the female was not present, egg and down characteristics (Klett et al. 1986). We distinguished the two species of scaup by using egg measurements (Bellrose 1980). We estimated the stage of incubation by candling several eggs from each nest (Weller 1956). We recorded the habitat type as meadow, floating vegetation, upland (forested or shrub), or island, and we estimated distance from the nest to the nearest open water, using the 30-m rope as a referent (Petrula 1994).

We returned to each marked nest at arbitrary intervals from 1 to 14 days until the nest was destroyed, abandoned, or successful ($\geq$ 1 egg hatched; Klett et al. 1986). During visits when the nest was active, we recorded the current number of eggs and their incubation stage. We also measured and numbered eggs that had been laid between visits at scaup nests. If the nest had been destroyed (i.e., several or all eggs missing, broken, or underwater and no female in attendance), we attempted to determine and record whether a predator or flooding was responsible. If the clutch was intact, but the eggs were cold

and the female was not present, we assumed that the nest had been abandoned. We did not record the nest fate as abandoned until the eggs remained cold and unattended for at least two visits. In such cases, we dated the failure to the first date when the eggs were found cold and unattended. If the nest had been abandoned between its discovery and the first revisit, we assumed that it was abandoned at discovery due to investigator disturbance. If at least one whole shell, egg membrane, or duckling was present in the nest bowl, we recorded the nest as successful.

Data Analysis

Our analysis included nest survival data collected 1989-1991 by Petrula (1994), 1992-1993 by MacCluskie (1997), and the data that we collected during the 2002-2003 breeding seasons. These data were collected using equivalent field methods on the same study site. We did not, however, attempt to identify trends in nest survival among years because of the 9-year span between our study and the previous studies.

We used an information-theoretic approach (Burnham and Anderson 1998) to obtain parameter estimates and evaluate the relative support for our predictions about the relationship of nest survival to the variables that we measured. We began by creating a set of candidate models that described our hypotheses about nest survival of ducks at Minto Flats. Each model represented the Daily Survival Rate (DSR) of the nest as a logit-linear function of some combination of species or tribe, year, habitat type, nest age, date, and distance to water. We considered additive relationships between DSR and these independent variables, as well as interactions between variables. We sought to create a

set of models that were interpretable in an ecological context, thoroughly addressed our predictions, and systematically described most of the plausible patterns of variation in nest survival at our study site.

We used three categorical variables: year, species, and habitat type. Diving duck species included in the analysis were canvasbacks, redheads (*Aythya americana*), lesser scaup, and greater scaup. Dabbling ducks were American wigeon, gadwalls (*Anas strepera*), green-winged teal (*Anas crecca*) mallards (*Anas platyrhynchos*), northern pintails (*Anas acuta*), and northern shovelers (*Anas clypeata*). Not all species were encountered in all years, however. To reduce the parameter space of our models, we defined four habitat types: meadow, floating vegetation, upland, and island. These habitat types reflected accurately the range of structural diversity of vegetation and accessibility of nest habitats to predators on the study area.

Each nest in the analysis was further defined by its age, date of discovery, and distance to open water. We estimated the age of the nest when found as the sum of number of eggs and estimated incubation stage of eggs (Klett et al. 1986). Nest age and date are somewhat confounded (Klett and Johnson 1982, Dinsmore et al. 2002); however, during our study, nests were initiated throughout the nesting season so we considered these variables separately. Distance to water, in meters, was used as a continuous individual covariate.

We used program MARK (White and Burnham 1999) to estimate parameters and evaluate the relative support for our candidate models. Differences in Akaike's

Information Criterion, corrected for finite sample size provided a basis for discrimination among competing models (ΔAIC_c; Burnham and Anderson 1998). Program MARK uses a generalized linear model (McCullaugh and Nelder 1989) with user-specified link function and error distribution to generate estimates of regression coefficients and their sampling variances and covariances. We used an extension of the survival models developed by Johnson (1979) and Bart and Robson (1982) that permits direct evaluation of the influence of covariates—including daily covariates like nest age—on DSR (Dinsmore et al. 2002). We used the logit link function and binomial error distribution, and did not interpret logit-scale regression coefficients if their 95% confidence intervals overlapped zero (Neter et al. 1996).

To assure accurate estimation of nest survival, this model requires that five general assumptions be fulfilled: (1) nest ages are correctly determined on the initial visit, (2) nest fates are known with certainty, (3) investigator activity does not influence nest fate, (4) fates of nests are uncorrelated, and (5) there is no heterogeneity in survival among nests (Dinsmore et al. 2002). To determine the age of nests at discovery, we used field-candling techniques (Weller 1956), and our field observations of successful nests indicated that this method was accurate. When we were uncertain about the fate of a nest, it was excluded from the analysis. We reduced the potential effect of our visits on nest survival by; (1) visiting nests in the late afternoon when the female was likely to be absent (Gloutney et al 1993), (2) scheduling revisits at 5-7 day intervals, and (3) spending as little time at the nest as possible. Furthermore, we did not use nests that were

abandoned between discovery and the first scheduled visit to estimate nest survival. We thought that assumptions four and five were probably violated during our study. Clustering of nests, particularly on islands, could have created some correlation of nest fates. Age and experience of the nesting females were unknown to us, and could have created heterogeneity among nest fates (Trauger 1971, Afton 1984). To correct for these infractions, we estimated a variance inflation factor ($\hat{c}$) from the most highly parameterized (global) model ($\hat{c}$ = deviance of the global model / df), and applied it to all estimates of sampling variance as well as AIC*c*. There are limitations to this method (Dinsmore et al. 2002), with the general outcome being that these estimates of $\hat{c}$ are positively biased with ordinary sample sizes (McCullagh and Nelder 1989:118); therefore, we probably over-inflated our sampling error by an unknown amount. Nevertheless, we used this method for lack of a currently viable alternative (Dinsmore et al. 2002, White 2002).

We used back-transformed estimates of DSR from our best-approximating model, $\hat{DSR}_i = \frac{1}{1+\exp(-(\hat{\beta}_0 + \hat{\beta}_1 X_{1i},...,\hat{\beta}_i X_{ni}))}$, where the $\hat{\beta}_i$ are the estimated regression coefficients from the model and the X_i are the date-specific values of the independent variables, to generate estimates of nest survival, assuming nesting periods of standard length (35 days for both species of scaup; Bellrose 1980, Klett et al. 1986). These estimates were the product of all of the daily survival rates predicted by the model, evaluated at the median, minimum, and maximum covariate values. We used the median

and the extremes, because covariates such as date and distance to water tended to have highly asymmetric (right –skewed) distributions, and we wanted to display accurately the full range of variation in nest survival rate for a given species. Sampling variances of nest survival were estimated with the Delta Method (Seber 1982:71).

We estimated average DSR (average of the annual estimates weighted by the inverse of their sampling variances; Schmutz and Morse 2000) among the seven years in our study and temporal process variation in DSR (total variance - sampling variance; Burnham et al. 1987: 260, Gould and Nichols 1998) to address the prediction that nest survival at our boreal forest study area would be similar on average, but less variable among years when compared with nest survival estimates from mid-continent studies.

RESULTS

We analyzed encounter history data from 1,821 duck nests (Table 1), of which 554 were scaup nests (127 greater scaup and 427 lesser scaup). Of all nests, 37% survived and 63% failed. The main apparent cause of nest failure for all species over all years was destruction by predators, 73 %, followed by flooding, 14%, abandonment, 8%, and 5% unknown causes. In some years, however, flooding of nests was a more important apparent cause of nest failure than predation (Table 1). In 1991, and 1992, flooding probably caused 31% and 49% of nest failures, respectively.

For scaup nests, we observed patterns of nest mortality similar to all other duck species. Thirty-five percent of scaup nests survived and 65% failed. Apparent causes of

nest failure for scaup were destruction by predators, 76%, flooding, 12%, abandonment, 8%, and 4% unknown causes.

Model Selection

The variance inflation factor ($\hat{c}$) estimated from the global model, DSR = Species + Habitat + (Species * Year) + (Habitat * Year), was 1.94. We adjusted AIC*c* values to quasi-AIC$_c$ (QAIC*c*) values (Table 2) and inflated the estimates of sampling error by a factor of $\sqrt{1.94} = 1.39$.

The best-approximating model indicated that DSR of nests varied among years, within seasons among years, among habitat types, and with distance to water (Table 2). DSR was highest in upland habitat, intermediate on islands, and lowest in meadows (Fig 2); floating vegetation was indistinguishable from meadow in terms of DSR (logit-scale difference = 0.157, SE = 0.407). A positive relationship between distance to water and DSR was estimated in the best approximating model, but the 95% confidence interval overlapped zero (0.150, SE = 0.09 on the logit scale). Within years, unique slope coefficients for trends with date were estimated; in 1993 and 2002 these trends were positive (Fig 3). Season trend coefficients had 95% confidence intervals that overlapped zero in all other years but in most years these coefficients were positive, but models with a common within-season trend coefficient for all years were not supported (ΔQAIC*c* >14). Models with quadratic within-season trends were not supported by the data (ΔQAIC*c* > 13).

Under the set of candidate models that we proposed for the data, species, tribe, and nest age were not strongly related to DSR of duck nests during our study. Parameterizations including species or tribe affiliations were not selected relative to other candidate models (ΔQAICc > 18; Table 2). We further proposed a model describing different DSR for scaup than other species (ΔQAICc = 126.40); this model received less support than a model of constant DSR across all variables (Table 2). Models depicting a relationship between nest age and DSR, whether unique to each year or common to all years, also received little relative support (Table 2). Taxonomic affiliation, however, remained important to us because species have been the practical units of management. Thus, when calculating nest survival, we returned to the specific values of covariates for scaup.

Nest Survival Estimates for Scaup

Because the model selection results indicated that variation among species was not related to nest survival, we combined observed covariate values for greater and lesser scaup and generated three estimates of nest survival for scaup in each year. These estimates represented the lowest, median, and highest nest survival possible for the nesting scaup that we observed. For instance, in a given year, the lowest nest survival estimate for scaup represented the earliest, closest to water scaup nest found in meadow habitat. The highest nest survival estimate in any year represented the latest, furthest from water scaup nest found on an island.

There was considerable variability in survival among nests; this variability was evident within as well as among seasons (Table 3). Minimum values of covariates resulted in nest survival estimates from 0.01 (95%CI: 0.00 to 0.03) in 1992 to 0.21 (95% CI: 0.13 to 0.30) in 2002. Estimates generated from median covariate values ranged from 0.01 (95% CI: 0.00 to 0.06) in 1992 to 0.61 (95% CI: 0.50 to 0.74) in 1993 (Fig 4). When maximum covariate values were incorporated, estimates ranged from 0.11 (95% CI: 0.02 to 0.47) in 1992 to 0.86 (95% CI: 0.77 to 0.96) in 1993.

Temporal Variation in Nest Survival.—Average annual DSR for all species of ducks at Minto Flats was 0.938 (95% CI: 0.919 to 0.957). Average annual nest survival (DSR^{35}; Johnson 1979) was 0.11 (95% CI: 0.05 to 0.22). Estimated annual process variation ($\hat{\sigma}$) in DSR was 0.02 (95% CI: 0.01 to 0.06). Adding two standard deviations ($2\hat{\sigma} = 0.04$) to average DSR (0.938) and raising the resulting DSRs to the 35th power indicated a range of annual nest survival from 0.02 to 0.46.

DISCUSSION

Patterns of Variation in Nest Survival

Patterns of variation in nest survival at Minto Flats were generally similar to those observed in other regions of North America. Destruction of nests by predators has been the prevailing apparent cause of duck nest failure in the prairie pothole region and the Canadian parklands (Johnson et al. 1992, Sargeant and Raveling 1992, Greenwood et al. 1995). Similarly, destruction by predators was the most common apparent cause of nest

failure at Minto Flats. Flooding of nests was also the apparent cause of many nest failures on our study site, but was probably of secondary importance.

Nests in meadow and floating vegetation habitat appeared relatively more vulnerable to destruction by nest predators than nests located on islands and in upland habitats. Meadow and floating vegetation habitats were accessible to all species of avian and mammalian nest predators, and in some years, were completely inundated by water after many nests had been initiated (Petrula 1994). Islands were likely less accessible to red foxes than mainland sites, but had little protection from flooding relative to upland habitats. Upland sites were probably less accessible to all predators and least vulnerable to flooding, as these habitats were associated with the greatest amount of structural complexity and topographic relief. Furthermore, there was prior evidence that species that primarily nested in upland habitats (e.g., green-winged teal, American wigeon) had slightly higher nest survival (Petrula 1994). Our observations of higher nest survival on islands and in forested habitats were consistent with results of other studies of nest survival of ducks conducted in the mid-continent (Sugden and Beyersbergen 1987, Lokemoen 1991, Johnson et al.1992, Lokemoen and Woodward 1992) and in the boreal forest (Trauger 1971, Fournier and Hines 2001).

Increasing survival of duck nests through the season is commonly attributed to the increasing abundance of alternative prey and phenology of nesting cover (Johnson et al. 1992, Grand 1995, Greenwood et al. 1995). Relationships between date and nest survival were variable among years at Minto Flats, but were positive in 1993 and 2002 and

positive at the point estimate in three of the remaining five years. The nesting seasons of 1993 and 2002 were characterized by extensive early-season flooding; perhaps a combination of decreasing risk of nest flooding and increasing abundance of alternative prey led to increasing nest survival through these seasons. Nevertheless, we cannot rule out the possibility that predator abundance declined during these seasons, or that other environmental factors caused the seasonal increase in nest survival.

Generally, species of duck has not been a strong predictor of nest survival (Higgins et al. 1992, Kantrud 1993, Greenwood et al. 1995, Fournier and Hines 2001). Predators most likely do not differentially prey upon the nests of different species nesting in similar habitats at similar times of the season, regardless of differences in nesting behavior (Johnson et al. 1992). Similarly, at Minto Flats, nest survival did not vary among species or between tribes during our study.

Nest age was not predictive of nest survival during our study. Nest ages in our sample were not distributed uniformly across the season, thus most potential confounding with date was very early and late in the season (Klett and Johnson 1982, Dinsmore et al. 2002). Perhaps nest age was not related to daily variation in nest survival because some older nests (≥17 days) became vulnerable to predators or flooding as a result of within-season dynamics. For instance, rising water levels and melting of ice pavements sometimes caused nest flooding, and low water levels made islands more accessible to predators (Petrula 1994). These events could have resulted in lower survival probability, independent of the age of the nest.

Duck Production in the Boreal Forest

Considerable annual variation in recruitment of ducks has been observed in mid-continent regions (Higgins et al 1992, Greenwood et al. 1995, Reynolds et al. 2001). This variation has been attributed to human-induced changes in predator communities and habitat conditions (Beauchamp et al 1996, Greenwood and Sovada 1996), as well as periodic cycles of drought (Karl et al. 1990). Conversely, the boreal forest has been characterized by relatively stable wetland conditions (Jessen 1981) and fewer human-induced changes in landscape composition and predator communities (Sargeant and Raveling 1992). Therefore, the boreal forest might be expected to exhibit consistent, albeit comparably lower (due to increased energetic cost of migration), production of ducks through time and across space (Pospahala et al. 1974, Calverley and Boag 1977, Johnson and Grier 1988, Rohwer 1992).

Although opportunities for renesting might be relatively limited in the boreal forest due to shorter ice-free periods, our study and other recent studies of clutch size and nest survival of ducks have indicated that the boreal forest has been more productive and dynamic than previously thought and support a revised view of duck production in this region (Petrula 1994, Grand 1995, Fournier and Hines 2001). Average clutch size of ducks nesting in boreal forest does not differ from clutch sizes of the same species of ducks nesting in the mid-continent (Bellrose 1980, Petrula 1994, Fournier and Hines 2001). Average nest survival rates of ducks in the boreal forest of Alaska and Canada has been similar to mid-continent observations, and have exhibited a comparable level of

variation across years (Higgins et al 1992, Grand 1995, Greenwood et al. 1995, Fournier and Hines 2001, Reynolds et al. 2001).

The amount of natural variation in a population parameter is strongly related to its influence on population dynamics (Hoekman et al. 2002). Variation in recruitment parameters, particularly nest and duckling survival (Cowardin et al. 1985, Johnson et al. 1992, Hoekman et al. 2002) has generally been much higher than variation in annual survival (Franklin et al. 2002) for most common North American duck species. Contrary to existing predictions about duck production in the boreal forest, temporal variation in nest survival of ducks (Range: 0.02 to 0.46) at Minto Flats was similar to spatio-temporal variation in nest survival of mid-continent mallards (Range: 0.00 to 0.31), while average rates of nest survival were similar (0.11 at Minto Flats and 0.13 in the mid-continent; Hoekman et al. 2002). As a result of this variability, nest survival was probably strongly related to production of scaup and other ducks at Minto Flats in most years, but knowledge of natural variation in other components of reproduction and survival would be needed to definitively rank its importance to population dynamics.

Nest Survival of Scaup.—Nest survival in the range of 15% to 20% has been indicated as necessary to maintain stable or increasing populations of mallards (Cowardin et al. 1985). Scaup most likely require higher nest survival than mallards for population growth because of the differences in life history between these species (Johnson and Grier 1988, Krementz et al.1997). For example, scaup generally have lower renesting rates and may have lower average breeding probability (Afton 1984, Koons 2001, Kessel

et al. 2002) than mallards (Hoekman et al. 2002). Estimates of median nest survival of scaup exceeded 20% only in 1993 and 2002, thus low nest survival could have limited the production of scaup during most years of our study.

This evidence is somewhat consistent with concurrent declines in abundance of scaup in interior Alaska (Hodges et al. 1996) and across the boreal forest (Wilkins and Otto 2003). Our study and other multi-year studies have revealed that nest survival of scaup has been highly variable among sites and years at several study areas in the boreal forest (Trauger 1971, Petrula 1994, Grand 1995, Fournier and Hines 2001). Thus, infrequent years when recruitment of scaup exceeds threshold levels for population maintenance or growth could be highly influential to the persistence of these populations. Observed variability in nest survival of scaup indicates that understanding the relationship between recruitment and population dynamics in these species will probably require estimation of recruitment parameters over multiple seasons across the entire boreal forest.

MANAGEMENT IMPLICATIONS

The relative importance of boreal forest habitats for breeding waterfowl has increased as habitat conversion and loss has occurred in the central prairies of U.S. and Canada. Recognition of the increased importance of boreal forest wetlands to continental waterfowl production and of the potential threats to this production posed by increased natural resource development and climate change (Kroneberg and Watt 2000) have caused organized efforts to conserve these important habitats (Zolkewich 1999).

The boreal forest appears to have been inaccurately characterized as less productive and variable than the prairie pothole region and the Canadian parklands (Johnson and Grier 1988). Revision of this characterization and estimation of recruitment at extensive spatial and temporal scales will probably be necessary to improve future management of scaup and other waterfowl species that breed in the boreal forest.

Minto Flats is an important area for breeding ducks, particularly lesser and greater scaup, in the boreal forest of interior Alaska (Hooper 1952, Rowinski 1958, Conant and Hodges 1985, Petrula 1994). Variation in nest survival of scaup and other common duck species indicates that Minto Flats has similar annual potential to produce ducklings as mid-continent regions (Higgins et al 1992, Greenwood et al. 1995, Reynolds et al. 2001). Thus, management activities directed toward maintaining existing habitat, informed by annual monitoring of production to elucidate the patterns and sources of variation in recruitment across the refuge would probably be the most effective strategy to support scaup populations at Minto Flats.

Furthermore, resource development is likely at Minto Flats. The Alaska Department of Natural Resources has approved oil and gas exploration at Minto Flats (Alaska Department of Natural Resources 2002). The effect of this exploration on nest survival of scaup at Minto Flats is likely to be related to the extent that exploration activity affects seasonal patterns of flooding (Petrula 1994) and accessibility of nesting

habitat to predators. This effect will be discerned only through research designed to measure and compare duck production among explored and unexplored areas.

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Table 1 – Total number, fate, and apparent causes of failure of duck nests found at Minto Flats, Alaska during 1989-1993, and 2002-2003.

				Cause of Failure			
Year	Total Nests	Successful	Failed	Predator	Abandoned	Flooded	Undetermined
1989	178	68	110	65	10	20	15
1990	317	97	220	206	9	0	5
1991	323	102	221	147	13	55	6
1992	119	20	99	22	9	68	0
1993	262	165	99	63	27	9	0
2002	332	149	183	139	12	5	27
2003	290	67	223	201	22	0	0

Table 2 – Models of Daily Survival Rate (DSR) of duck nests found at Minto Flats, Alaska during 1989-1993 and 2002-2003. Models are ranked by differences in Quasi-AIC values (ΔQAIC*c*).

DSR Model[a]	K[b]	-2logL	ΔQAIC*c*
DW[c] + Habitat + Year * T[d]	18	3500.77	0.00
Habitat + Year * T	17	3507.17	1.27
Year + DW + Habitat	13	3538.00	9.07
Year + Habitat + TT[e]	13	3546.06	13.23
Year + T + DW + Habitat	12	3551.85	14.19
Species + Year * T	22	3520.66	18.37
DW + Habitat + Year * Nest Age	18	3536.57	18.45
Year + Nest Age	8	3588.01	24.77
Year + Tribe + Habitat	11	3579.25	26.30
Year	7	3624.51	41.57
Global	81	3391.61	74.44
Constant	1	3808.60	124.42
Species + Scaup	2	3808.55	126.40

[a] The "+" between variables indicates an additive effect; the "*" denotes interaction.

[b]Number of parameters.

[c]Distance to water.

[d]Logit-linear trend with season date.

[e]Quadratic trend with season date.

Table 3- Nest survival of greater and lesser scaup ($\hat{S} \pm SE$) at Minto Flats, Alaska during 1989-1993, and 2002-2003. Each estimate represents the combination of habitat, season date, and distance to water that would lead to the minimum, median, and maximum observed nest survival rate for that year.

	$\hat{S}$		
Year	Minimum	Median	Maximum
1989	0.02 ± 0.02	0.07 ± 0.03	0.30 ± 0.11
1990	0.02 ± 0.01	0.05 ± 0.02	0.33 ± 0.13
1991	0.02 ± 0.01	0.10 ± 0.04	0.20 ± 0.11
1992	0.01 ± 0.01	0.01 ± 0.01	0.11 ± 0.09
1993	0.13 ± 0.06	0.61 ± 0.06	0.86 ± 0.05
2002	0.21 ± 0.04	0.27 ± 0.06	0.69 ± 0.10
2003	0.03 ± 0.04	0.04 ± 0.02	0.18 ± 0.04

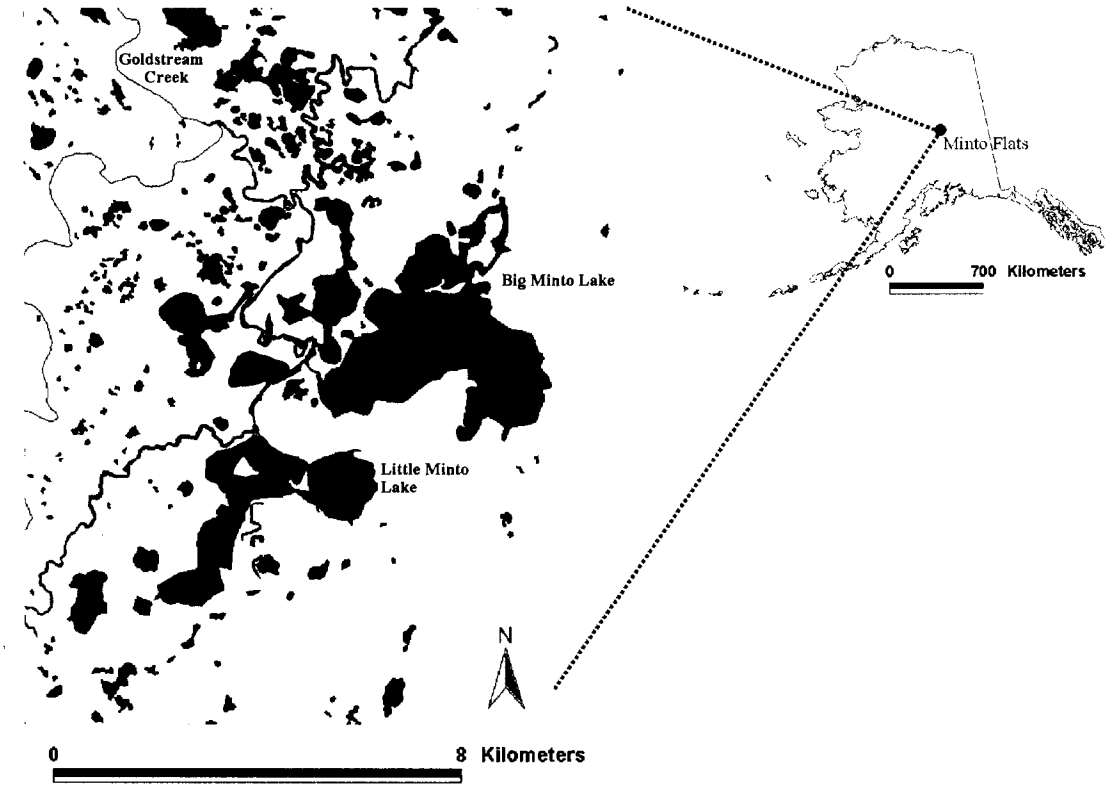

Figure 1- Minto Lakes study site at Minto Flats, Alaska. Black areas represent open water, and white areas represent land, at average water levels.

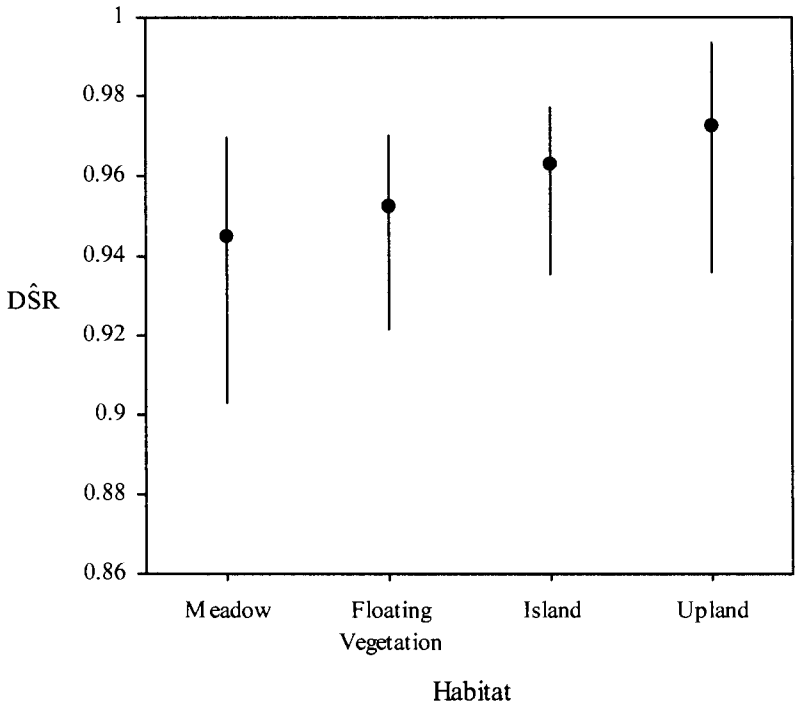

Figure 2 – Daily Survival Rate (DSR) of duck nests in different habitats at Minto Flats, Alaska during 1989-1993 and 2002-2003. Error bars represent 95% confidence limits.

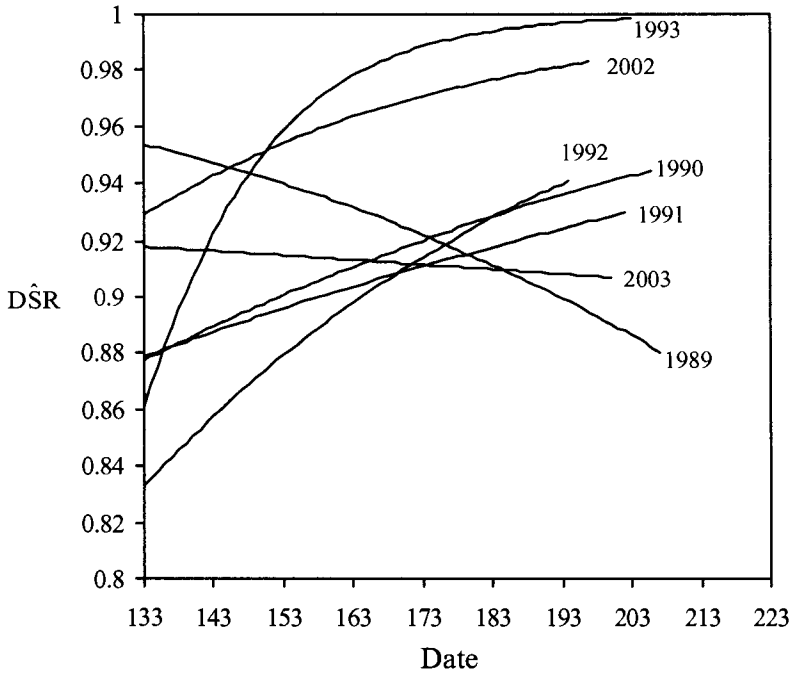

Figure 3- Within-season trends in Daily Survival Rate (DSR) of duck nests at Minto Flats during 1989-1993 and 2002-2003. Trends for 1993 and 2002 were estimated with confidence intervals that did not overlap zero. Variation in intercepts represents among-year variation in DSR. Date is the number of days since 1 January.

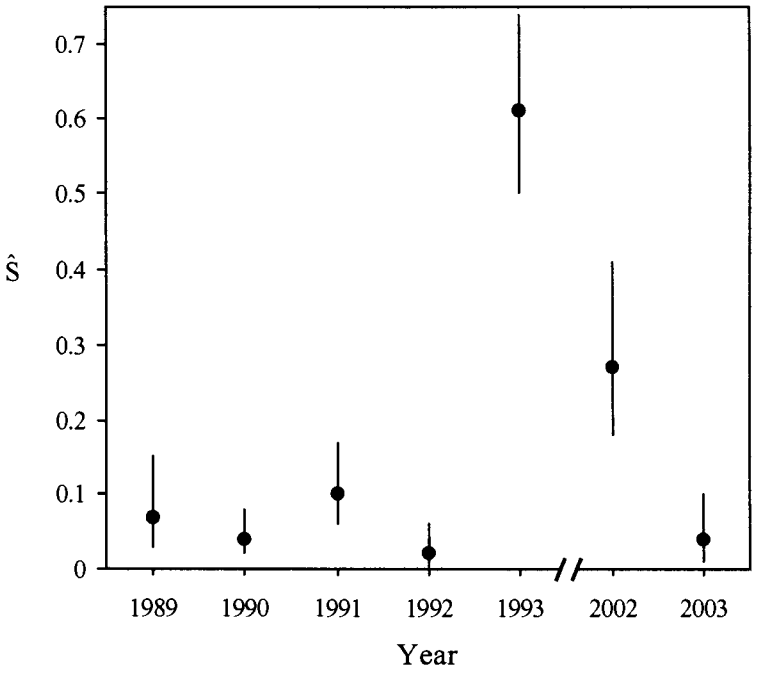

Figure 4 – Nest survival of scaup (greater and lesser combined) at Minto Flats, Alaska during 1989-1993 and 2002-2003. Error bars represent 95% confidence limits.

SURVIVAL OF SCAUP DUCKLINGS AT MINTO FLATS, ALASKA

Abstract: We studied duckling survival of lesser (*Aythya affinis*) and greater (*A. marila*) scaup at Minto Flats, Alaska during 2002-2003. We captured and marked 42 female scaup during the study, and subsequently monitored survival of 31 scaup broods with 284 ducklings. Daily Survival Rate (DSR) of ducklings varied between years and was positively related to female body condition and duckling age. Estimated duckling survival to 30 days for both species of scaup was 0.24 (95% CI: 0.16 to 0.36) in 2002 and 0.03 (95% CI: 0.00 to 0.19) in 2003. Most of the variation in duckling survival between years was probably related to high rates of predation by gulls (*Larus spp.*) during 2003. Estimated recruitment of female scaup to 30 days (clutch size * nest survival * duckling survival * 0.5) was 0.30 (SE = 0.19) in 2002 and 0.01 (SE = 0.01) in 2003. We conclude that management to maintain existing habitat for breeding scaup, and identify and mitigate any negative effect of human activity during the breeding season, is the most likely way to support recruitment of scaup at Minto Flats. Furthermore, we suggest that

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annual monitoring of scaup production at multiple sites across the boreal forest is probably the most feasible way to determine whether low recruitment rates are responsible for declines in the abundance of scaup.

Key Words: Alaska, *Aythya affinis*, *Aythya marila*, boreal forest, ducks, duckling survival, population dynamics, recruitment, scaup.

INTRODUCTION

The rate of recruitment of juveniles to the fall population has had substantial influence on the population dynamics of mallards (*Anas platyrhynchos*), canvasbacks (*Aythya valisineria*), and lesser scaup in the prairie pothole region, Canadian parklands, and boreal forest of North America (Johnson et al. 1992, Anderson et al. 1997, Anderson et al 2001, Koons 2001, Brook 2002, Hoekman et al. 2002). Consequently, studies of reproductive success and its components are likely to provide useful information for management of these duck populations, particularly when decreasing trends in indices of recruitment attend long-term declines in abundance (Johnson and Shaffer 1987, Austin et al. 2000).

A recent decline in abundance of the combined population of lesser and greater scaup has been accompanied by declines in the ratio of juvenile to adult lesser scaup in the annual harvest, indicating that reduced recruitment of lesser scaup has likely contributed to the decline (Afton and Anderson 2001). Recruitment of scaup has not

been thoroughly studied in the boreal forest region where the majority of North American lesser scaup breed, however (Austin et al 1998, Kessel et al. 2002).

The process of recruitment in duck populations comprises several life-history parameters and each is subject to variation with ecological conditions (Chapter 1). Of the components of recruitment, nest and duckling survival have exhibited the most natural variation in a variety of species—including scaup—across their breeding ranges (Afton 1984, Grand and Flint 1996, Austin et al. 1998, Guyn and Clark 1999, Anderson et al. 2001, Kessel et al. 2002). Therefore, these parameters are likely to exert substantial influence on recruitment (Johnson et al. 1992, Hoekman et al. 2002).

Existing information about clutch size (Trauger 1971, Petrula 1994) and nest survival (Trauger 1971, Petrula 1994, Grand 1995, Fournier and Hines 2001, Chapter 1) of scaup in the boreal forest indicated that patterns of variation in these parameters have been similar to those observed for lesser scaup in mid-continent regions (Afton 1984, Koons 2001). Estimates of duckling survival, however, are rare for either species of scaup (Austin et. al 1998, Kessel et al. 2002). Moreover, little information is available about relationships between duckling survival of scaup and ecological conditions (Afton 1984, Koons 2001, Brook 2002). Investigation of duckling survival of scaup in the boreal forest was therefore necessary to improve the general understanding of recruitment in these species.

We studied duckling survival of greater and lesser scaup at Minto Flats, Alaska during 2002-2003. Studies of a variety of dabbling (*Anas* spp.) and diving (*Aythya* spp.)

duck species across North America indicate that duckling survival decreases with predation risk, exposure to precipitation, and exposure to low temperatures (Johnson et al. 1992, Flint and Grand 1996, Korschgen et al.1998, Guyn and Clark 1999, Pietz et al. 2003). Therefore, we predicted that duckling survival of scaup at Minto Flats would be related to ecological factors that were directly or indirectly related to variation in these primary sources of mortality.

Because predator abundance and activity, availability of alternative prey, and environmental conditions vary among years (Johnson et al. 1992, Flint and Grand 1996, Pietz et al. 2003), we predicted that duckling survival would vary between years. Additionally, we thought that within-season variation in mortality risk was likely. We predicted that duckling survival would increase with season date because most wetlands at Minto Flats are permanent or semi-permanent, and predation by gulls was likely to decrease through the season (Johnson et al. 1992, Flint and Grand 1996). Most mortality of ducklings occurs in the first two weeks post-hatch (Johnson et al 1992, Korschgen et al 1998); thus, we predicted that duckling survival would increase with age. We predicted that duckling survival would vary between greater and lesser scaup if habitat use or brood care differed between these species (Johnson et al. 1992). Females in better physical condition post-incubation might devote more time to brood care (Johnson et al 1992, Yerkes 2000, Gendron and Clark 2002); we predicted that duckling survival would increase with female body condition. Duckling survival may decrease with distance of overland movements (Rotella and Ratti 1992, Leonard et al. 1998), and we predicted that

the negative effect of these movements might be greatest during the initial movement from the nest to water. Precipitation events and low temperatures have been associated with decreased duckling survival (Korschgen et al. 1998, Pietz et al. 2003). We predicted that duckling survival would decrease with precipitation, and increase with minimum temperature.

STUDY AREA

We conducted our investigation of duckling survival in an approximately 30 square kilometer area immediately surrounding Big and Little Minto Lakes (Figure 1). General characteristics of the Minto Flats State Game Refuge (64°50′N, 148°50′W) are described in Chapter 1.

At Minto Flats, brood-rearing habitat for waterfowl consists of emergent zones dominated by manna grass (*Glyceria spp.*) that vary in extent with water levels, and low-lying meadows of bluejoint grass (*Calamagrostis canadensis*) and sedge (*Carex spp.*) Larsen (1997) and Petrula (1994) provided a comprehensive description of the vegetation communities and habitat characteristics of Minto Flats.

Several species of known duckling predators (Bellrose 1980, Sargeant and Raveling 1992) are common at Minto Flats (Alaska Department of Fish and Game 1992, Petrula 1994). Mew (*Larus canus*) and herring gulls (*L. argentatus*) nested on the study area and commonly preyed on ducklings (J. Walker pers. obs.). Red fox (*Vulpes vulpes*) and mink (*Mustela vison*) are known mammalian predators of ducklings (Korschgen et al. 1996) and are common at Minto Flats (Rowinski 1958, Petrula 1994). Northern pike

(*Esox lucius*) also likely account for some mortality of young (< 1 week of age) ducklings (Kessel et al. 2002).

METHODS

Data Collection

Capture and Marking of Females.—To fulfill both major objectives of our project (estimation of nest and duckling survival) we searched for nests daily, by dragging a 30-m rope through the cover to flush the female from the nest, from the third week of May until the second week of July 2002-2003 (Chapter 1). When we observed pipping eggs (1-2 days before estimated hatch date), we captured the incubating female on her nest by using a sliding-door trap made of 2.54 cm wire mesh (Weller 1957). Upon capture, we recorded culmen, head, and tarsus length (± 0.1mm) using dial calipers and mass (± 5g) using a Pesola spring scale. Captured females were then marked with a U.S. Fish and Wildlife Service leg band, nasal discs bearing a unique alphanumerical code (Lokemoen and Sharp 1985), and a 9-g, back-mounted VHF transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). The transmitter was held in place by a subcutaneous wire prong and Vetbond® veterinary adhesive (Mauser and Jarvis 1991, Pietz et al. 1995). Last, to reduce the likelihood of nest abandonment, we lightly anesthetized the female with Metofane® and placed her next to the nest (Rotella and Ratti 1990). The Institutional Animal Care and Use Committee of the University of Alaska Fairbanks sanctioned all capture and marking techniques (permit number: 02-05).

Relocation and Duckling Counts.— To obtain initial brood counts, we revisited the nests of marked females one day after hatch and counted unhatched eggs, membranes, and capsules. Thereafter, we relocated marked females every three days until the brood reached 15 days of age and every seven days from 15-30 days of age (7-10 observations). We used 60-power spotting scopes to obtain a count of the ducklings during relocations. If we were unable to obtain a complete count, we located the brood the following day and each consecutive day until the count was certain. Only counts where the female and ducklings were observed together in open water were used to estimate duckling survival. When females were observed with no ducklings, we continued to relocate them for at least three intervals (9 to 21 days) to confirm brood loss. We further recorded a binary index of disturbance during each visit (1 = flushed female from ducklings, 0 = female not flushed) for use in modeling any effect of our observation on duckling survival. We terminated duckling counts for the purpose of survival estimation when ducklings reached 30 days of age; brood mixing became common past this point, and females appeared to be abandoning their broods. Thus mortality, emigration to other broods, and abandonment were completely indistinguishable past 30 days.

Data Analysis

We used an information-theoretic approach (Burnham and Anderson 1998) to estimate parameters and evaluate the relative support for our predictions about the relationship of duckling survival to the covariates. We began by creating a set of candidate models that represented our hypotheses about duckling survival. Each model

represented the Daily Survival Rate (DSR) of the duckling as a logit-linear function of some combination of: year, date, brood age, species, female body condition, distance from the nest to water, daily precipitation, and daily minimum temperature. We considered additive relationships between DSR and these independent variables, as well as interactions between variables. We sought to create a set of models that were interpretable in an ecological context, thoroughly addressed our predictions, and systematically described most of the plausible patterns of variation in duckling survival at our study site.

Binary explanatory variables in the analysis were year (2002 or 2003), species (greater or lesser scaup), and investigator disturbance. Date, duckling age (1-30 days), female condition index, distance from the nest to water, daily precipitation, and daily minimum temperature were continuous variables. We indexed physical condition of females by regressing mass against the first principal component axis of head, culmen, and tarsus length (structural size) for each year and using the residuals from these regressions as individual covariates in the models (Sedinger et al. 1997, Gendron and Clark 2002). Distance from the nest to water was estimated in meters for the interval between hatch and the first post-hatch observation only. Daily minimum temperature and daily precipitation were obtained from a NOAA weather station (CHTA2), located on Minto Flats, approximately 3 km north of the study site. Precipitation and minimum temperature were input as daily-incrementing group covariates.

We used program MARK (White and Burnham 1999) to estimate DSR of ducklings and evaluate the relative support for our candidate models. Differences in Akaike's Information Criterion (ΔAIC_c; Burnham and Anderson 1998), corrected for finite sample size, provided the basis for discrimination among competing models. To estimate daily survival rate (DSR) of ducklings, we used generalized linear models (McCullaugh and Nelder 1989) with a binomial error distribution and logit link function to generate estimates of regression coefficients and their sampling variances and covariances. This extension of the survival models developed by Johnson (1979) and Bart and Robson (1982) permits direct evaluation of the influence of covariates—including daily covariates such as precipitation—on DSR (Dinsmore et al. 2002). We did not interpret logit-scale regression coefficients if their 95% confidence intervals overlapped zero (Neter et al. 1996).

Accurate estimation of DSR requires that five general assumptions be fulfilled: (1) duckling ages are correctly determined, (2) duckling fates are known with certainty, (3) investigator activity does not influence fate, (4) fates of ducklings within broods are uncorrelated, and (5) there is no heterogeneity in survival within or among broods (Dinsmore et al. 2002). We determined accurately the age of ducklings by revisiting nests one day after hatch. We were reasonably confident that losses of ducklings represented mortality rather than emigration to other broods. Some losses of ducklings could have been due to one or two ducklings joining other broods (e.g., Mauser et al.1996), but our extensive observations of ducklings indicated that (1) brood-mixing

usually involved one or two females attending a combined brood; (2) no marked females gained ducklings before broods were 25 days of age; and (3) few unmarked broods were observed with ducklings of variable age (Gollop and Marshall 1954). We used the disturbance index to investigate the effect of flushing the female from the brood, and we maintained a distance of > 75 meters when counting ducklings. To correct for lack of independence of duckling fates within broods and heterogeneity among and within broods, we estimated a variance inflation factor ($\hat{c}$) from the most highly parameterized (global) model ($\hat{c}$ = deviance of the global model / df), and applied it to all estimates of sampling variance and AIC*c*.

To generate estimates of duckling survival to thirty days, we used back-transformed estimates of DSR from our best-approximating model,

$$\hat{DSR}_i = \frac{1}{1+\exp(-(\hat{\beta}_0 + \hat{\beta}_1 X_{1_i},\ldots,\hat{\beta}_i X_i))}$$, where the $\hat{\beta}_i$ are the estimated regression coefficients from the model, and the X_i are the date-specific values of the independent variables. These estimates were the product of all of the daily survival rates predicted by the model, incremented over brood age from 1 to 30 days, at the mean female condition, for both years. Sampling variances of duckling survival were estimated with the Delta Method (Seber 1982:71).

We estimated recruitment of female scaup ducklings to thirty days of age (among the nests in our sample) as the product of clutch size, nest survival, and duckling survival assuming a 1:1 sex ratio at hatch (Bellrose 1980). To complete this product, we used

estimates from our concurrent investigation of clutch size and nest survival of scaup at Minto Flats. We assumed independence of parameters within years. Sampling variance was estimated using a modification of the Goodman (1960) method (Brown et al. 1993).

RESULTS

We marked 41 female scaup during 2002-2003 and 32 were used for duckling observations; 9 nests failed in the interval between marking and hatching. Sixteen lesser scaup females with 157 ducklings and 6 greater scaup females with 52 ducklings were monitored from 6 July to 17 August 2002. Five lesser scaup females with 40 ducklings and 5 greater scaup females with 35 ducklings were monitored from 5 July to 10 August 2003. At least one duckling survived to thirty days of age in 5 of the 22 broods observed in 2002. In 2003, 1 of 10 broods had a surviving duckling at thirty days. Total brood loss during one interval occurred in 6 of 22 broods in 2002 and 2 of 10 broods in 2003. In 2002, predators killed two females during brood rearing; one female was killed in 2003. Survival of marked females during the observation period was 0.80 (95% CI: 0.43 to 0.95).

Model Selection

The variance inflation factor ($\hat{c}$) estimated from the global model was 2.68. The global model included additive effects of all covariates, interaction between brood age and minimum temperature, interaction between brood age and precipitation, and interaction between brood age and disturbance. We adjusted AIC*c* values to quasi-AIC*c*

(QAIC*c*) values (Table 1), and inflated the estimates of sampling error by a factor of $\sqrt{2.68} = 1.64$.

The best-approximating model, DSR = Year + Age + Body Condition, indicated that duckling survival rate varied between years, with duckling age, and with female body condition (Table 1). The estimated difference in DSR between 2002 and 2003 was 0.96 (SE = 0.24) on the logit scale. Duckling age and female body condition were positively related to DSR in both years (Figs. 1 and 2). Logit-scale slope coefficients for brood age and female body condition were 0.15 (SE = 0.03) and 0.35 (SE = 0.13).

Selection uncertainty existed among the top three models (Table 1). We observed weak support for an interaction between brood age and year (ΔQAIC*c* = 0.22), however, the 95% confidence interval for the estimated difference between the year-specific age coefficients (0.10; 95% CI: -0.03 to 0.23) overlapped zero. The effect of precipitation on DSR (-0.26; 95% CI: -1.35 to 0.83) was also not estimated precisely enough to permit reliable inference. Our models did not support predicted relationships between DSR and date, species, distance from the nest to water, disturbance, or minimum daily temperature (ΔQAIC*c* > 7.0; Table 1).

Duckling Survival and Recruitment to 30 days.—Duckling survival to 30 days was 0.24 (SE = 0.05) in 2002 and 0.03 (SE = 0.04) in 2003. Clutch size of scaup at Minto Flats was 9.4 (SE = 0.04; n = 79) in 2002 and 9.1 (SE = 0.04; n = 73) in 2003. Nest survival was 0.27 (SE = 0.06) in 2002 and 0.04 (SE = 0.02) in 2003. Recruitment of

female scaup to 30 days (clutch size * nest survival * duckling survival * 0.5) was 0.30 (SE = 0.19) in 2002 and 0.01 (SE = 0.01) in 2003.

DISCUSSION

Patterns of Variation in Duckling Survival

Annual variation in duckling survival has been commonly observed in multi-year studies regardless of regions and species (Johnson et al. 1992, Grand and Flint 1996, Gendron and Clark 2002). Similarly, we observed considerable variation in duckling survival of scaup between years at Minto Flats. There was little evidence that daily minimum temperature, precipitation, or their interaction, could explain the annual variation in duckling survival; average minimum daily temperature was 7.2° C (SD = 2.6° C) in 2002 and 10.1° C (SD = 3.9° C) in 2003. Furthermore, although total precipitation was 25.5cm in 2003 and 4.3cm in 2002, models of interaction between precipitation and year were not supported ($\Delta QAIC_c = 43.98$). Indirect effects of environmental dynamics might have also manifested as relationships between duckling survival and date, but duckling survival was not related to date at Minto Flats. In other studies, relationships between duckling survival and season date have been attributed to within-season changes in wetland conditions (Johnson et al. 1992, Pietz et al. 2003); however, wetlands at Minto Flats do not decline in number through the season (Petrula 1994). Therefore, we speculated that between-season variation in predation risk, rather than direct environmental effects, might have produced most of the variation that we observed.

The extremely low duckling survival that we observed in 2003 might have been the result of large numbers of gulls and scaup nesting on islands together. Many islands that were completely underwater during 2002 were available for nesting during 2003 and were used by both gulls and scaup (J. Walker pers. obs.). Nesting in gull colonies is common among scaup nesting in northern regions and may result in increased nest survival rate because gulls and other larids tend to defend nesting areas from mammalian predators (Trauger 1971, Fournier and Hines 2001). However, gulls prey upon ducklings extensively; any benefits of nesting among larids may be reduced when newly hatched ducklings are subsequently subjected to high rates of predation (Vermeer 1968, Dwenychuk and Boag 1972, Lynch and Toepfer 1975). Direct examination of these relationships could provide useful information about scaup recruitment in the boreal forest.

Daily survival of ducklings increased with age in both years of our study. Increasing duckling survival with age has been observed in studies of many species of North American ducks in both mid-continent and northern regions (Johnson et al. 1992, Dawson and Clark 1996, Korschgen et al. 1998, Guyn and Clark 1999). Possibly, vulnerability of ducklings to predation decreased as ducklings became larger and better able to escape predators or simply became too large for predators to consume (Johnson et al.1992). Individual heterogeneity in survival could also have contributed to this relationship (Rexstad and Anderson 1993).

Ducklings accompanied by females in better condition had higher survival rates during our study. Positive relationships between female condition and duckling survival have been observed in redheads (*Aythya americana*), gadwall, and common pochards (*Aythya ferina*; Blums et al. 1997, Gendron and Clark 2002, Yerkes et al. 2002). Other researchers observed no relationship between female mass and duckling survival in mallards (Orthmeyer and Ball 1990) and canvasbacks (Arnold et al. 1995). Afton (1984) observed that female lesser scaup with broods spent less time feeding than females without broods. Females that maintained better physical condition through incubation might have spent less time feeding during brood-rearing, and thus, been more attentive to their broods (Talent et al 1983).

Species-specific variation in duckling survival has been observed in Saskatchewan where gadwalls have had higher duckling survival than mallards; however, these species have different nesting chronology and diets (Gendron and Clark 2002). Greater and lesser scaup at Minto Flats have similar nesting chronology and, most likely, similar diets (Petrula 1994, Kessel et al. 2002). Accordingly, any difference in survival of ducklings between these species probably would have resulted from differences in brood-rearing behavior. Brood-rearing behavior tends to be similar between scaup species, however (Austin et al. 1998, Kessel et al 2002).

In previous studies, the relationship between duckling survival and brood movements has been variable. Several investigators have reported no effect of distance traveled for mallard and gadwall broods (Talent et al. 1983, Dzus and Clark 1997,

Gendron and Clark 2002); however, Rotella and Ratti (1992) and Leonard et al. (1998) reported negative correlation for mallard and canvasback. Dzus and Clark (1997) suggested, as an explanation for this discrepancy, that beyond some minimum distance, the energetic costs and increased predation risk of movement could result in decreasing survival. At Minto Flats, we observed no relationship between distance from the nest site to water and duckling survival. Initial movements of scaup broods from the nest to water ranged from 5m to 70m during our study. These movements were much shorter than observed movements in other studies, and perhaps even the longest were short enough to have little effect on survival.

Duckling Survival and Recruitment

Duckling survival.—Duckling survival of scaup at Minto Flats during 2002-2003 was low compared to estimates from most recent studies of mallards, gadwalls, and northern pintails (*Anas acuta*) conducted in the prairie regions of the north-central US and south-central Canada (Dzus and Clark 1997, Guyn and Clark 1999, Gendron and Clark 2002, Pietz et al 2003). Estimated duckling survival rates of redheads, canvasbacks, and lesser scaup from mid-continent regions have been similar to the level of duckling survival that we observed in 2002 (Dawson and Clark 1996, Korschgen et al 1998, Yerkes 2000, Koons 2001). Part of the discrepancy in duckling survival between these dabbling and diving duck species might be explained by differences in brood-rearing behavior. That is, diving duck young may be more vulnerable to predators and exposure because female diving ducks frequent large wetlands, which generally have less

emergent cover (Hines 1977, Stoudt 1982, Decarie et al. 1995), and are generally less wary during brood-rearing than dabbling ducks (Smith 1971).

Intertribal variation in brood –rearing behavior is not sufficient to explain the low levels of duckling survival that we observed. Duckling survival of greater scaup on the Yukon-Kuskokwim (Y-K) Delta in Alaska was similar to or higher than the rates that we observed at Minto Flats in 2002 (Kessel et al. 2002), but survival of northern pintail ducklings on the Y-K Delta was lower than our 2002 estimates during 1991-1992, and was comparable to our 2003 estimates during 1993 (Grand and Flint 1996). In general, duckling survival has been lower in these northern breeding areas than in mid-continent regions. Regional differences in duckling survival might be related to differences in predator communities and timing of reproductive events (e.g., mean hatch date) in northern regions.

Recruitment to 30 days.—Although our index of recruitment is missing several parameters, there is little doubt that recruitment of scaup was very low during our study. If breeding-season survival of females and egg hatchability were 1.0, all females present on the study area nested, and 17% of females renested after their first unsuccessful attempt (Afton 1984) our estimates of recruitment would only increase by 17%. Thus, even if these unrealistic assumptions were fulfilled, at the recruitment rates we observed in 2002, the females in our sample would still have required approximately three years to produce one female recruit to thirty days; at 2003 rates, they would have required 100

years. Estimated life expectancy of female scaup, i.e., $-1/\ln(\hat{S})$, is between one and three years at average survival rates (Austin et al. 1998, Kessel et al. 2002).

Our observations of unmarked females killed on nests and survival estimates of marked females during the brood-rearing period verified that there was mortality of females during the breeding season. Probability of breeding and survival of eggs have tended to be variable in other studies of scaup production (Austin et al. 1998, Kessel et al. 2002). In studies of lesser scaup, the probability of breeding varied with age and habitat conditions in both Manitoba (Afton 1984) and Northwest Territories (Trauger 1971). Fournier and Hines (2001) observed egg hatch rates of 0.98 in Northwest Territories. Furthermore, due to the shorter nesting season at Minto Flats (Petrula 1994) it is unlikely that females renested as often as in Manitoba (Afton 1984). Therefore, because our estimates of recruitment did not include the entire suite of recruitment parameters, they probably represented an upper bound on recruitment of scaup during 2002-2003. Nevertheless, they serve to further illustrate the high level of variation in recruitment of scaup at our site in the boreal forest.

This two-year study could not reveal the full extent of temporal variation in recruitment of scaup at Minto Flats or the extent of spatial variation in interior Alaska, much less the boreal forest. During our study, recruitment of scaup at Minto Flats had probably dropped to levels of concern to waterfowl managers and, if locally and temporally consistent, could partially explain recent long-term declines in abundance of scaup in interior Alaska (Hodges et al. 1996, Kessel et al. 2002). Alternatively, we might

have observed a period during which an extremely poor year for scaup reproduction followed a more typical year. Estimation of all recruitment parameters at larger spatial and temporal scales would be required to assess reliably whether low recruitment rate of scaup was responsible for regional or continental declines in abundance.

MANAGEMENT IMPLICATIONS

Minto Flats is an important area for scaup production in the boreal forest of interior Alaska (Hooper 1952, Rowinski 1958, Conant and Hodges 1985, Petrula 1994, Kessel et al. 2002); however, annual variability in production, likely related to varying predator abundance, water levels, and timing of reproduction, has been high (Petrula 1994) with many years probably resulting in little recruitment. These patterns of variation are more consistent with current ideas about duck production in mid-continent regions than commonly accepted hypotheses about duck production in the boreal forest (Calverly and Boag 1977, Petrula 1994, Johnson and Grier 1988). Therefore, management of scaup at Minto Flats will probably be most effective when targeted toward conservation of existing habitat (Kadlec and Smith 1992).

Minto Flats has historically been relatively free of the impacts of disturbance (Alaska Department of Fish and Game 1992), but human population growth in the area, increased interest in resource development, and climate change could affect future waterfowl production. Because of its proximity to Fairbanks, Minto Flats is a popular destination for anglers, campers, and aviators during the breeding season of scaup and other waterfowl. Negative effects of increased human activity on reproductive success of

waterfowl during the breeding season have been well documented. Most important breeding areas in the mid-continent are closed to recreation during all or part of the breeding season as a result (US Fish and Wildlife Service 1976, Braun et al. 1978, Dahlgren and Korschgen 1992). Although the effect of human activity on waterfowl production at Minto Flats is unknown, it seems likely to be negative in light of existing evidence; possibly, closure of areas that have the highest density of scaup during the breeding season would be a useful management strategy for Minto Flats. Exploration for petroleum and natural gas has also been recently approved on most of Minto Flats (Alaska Department of Natural Resources 2002) and might affect duck production through disturbance and habitat alteration if patterns of seasonal flooding and access to the refuge are changed. Additionally, the climate of the boreal forest is changing with unknown effect on the production of scaup; however, environmental changes are likely to result from climate change (Kroneberg and Watt 2000). For example, longer ice-free periods at Minto Flats would allow a longer breeding season for scaup, but could also be associated with an increase in the abundance of predators. Thus, given the recent declines in abundance of scaup in interior Alaska (Hodges et al. 1996) and the great annual variability in nest and duckling survival that we observed during our study, management efforts to understand the impacts of resource development, climate change, and recreational use on scaup production and efforts to mitigate these effects when they are negative are warranted (Zolkewich 1998, Kroneberg and Watt 2000, Alaska Department of Natural Resources 2002). Such management decisions could be based on

comparisons of annual scaup production at Minto Flats in areas without disturbance, and areas subject to resource development, recreational activity, or both. Nevertheless, the current status of North American scaup populations indicates that some restriction of recreational access to breeding areas during the nesting and brood-rearing period is warranted. Moreover, annual monitoring of production at regional scales (i.e., at several locations across the boreal forest) is probably necessary to understand and identify effects of spatial and temporal variation in recruitment on the population dynamics of North American scaup and effectively manage these species.

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Table 1 – Models of Daily Survival Rate (DSR) of lesser and greater scaup ducklings at Minto Flats, Alaska. Models are ranked by differences in Quasi-AIC values ($\Delta QAIC_c$).

DSR Model[a]	K[b]	-2logL	$\Delta QAIC_c$
Year + Age + Body Condition	4	749.96	0.00
Body Condition + Year * Age	5	745.07	0.22
Year + Age + Body Condition + Ppt.[c]	5	749.44	1.85
Age + Body Condition + Ppt.	4	744.34	5.38
Year + Species + Age	4	770.15	7.53
Age + Body Condition + DW[d] + Ppt.	5	769.27	9.25
Age + Body Condition + T[e]	4	775.27	9.44
Global	14	721.01	12.36
Age * Min. Temp.[f]	4	787.57	14.04
Constant	1	950.64	68.80
Investigator Distubance[g]	2	949.43	70.36

[a] The "+" between variables indicates an additive effect; the "* " denotes interaction.

[b] Number of parameters.

[c] Daily precipitation (cm).

[d] Distance from nest to water.

[e] Logit-linear trend with season date.

[f] Minimum daily temperature.

[g] Indicator variable 1 = female flushed from brood, 0 = female not flushed.

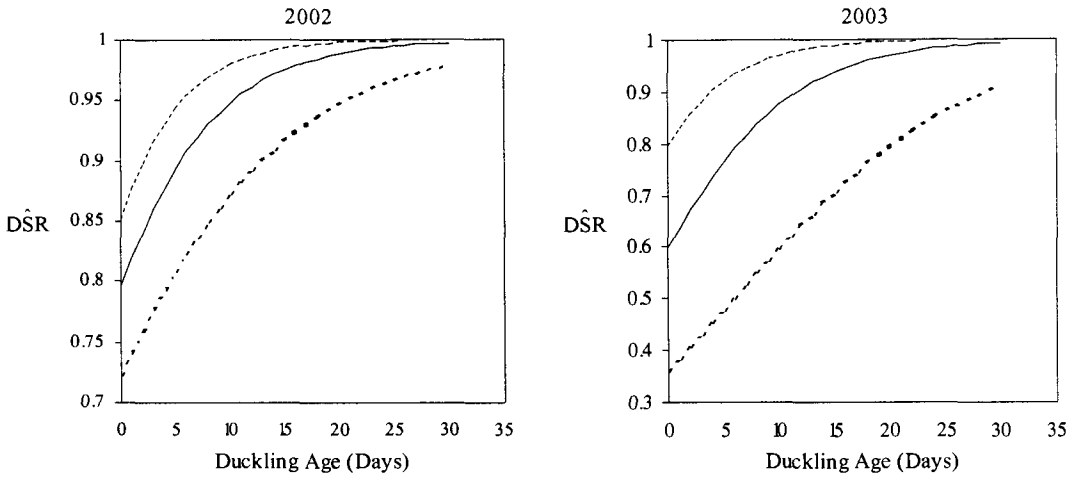

Figure 1 - The relationship between age and Daily Survival Rate (DSR) of lesser and greater scaup ducklings at Minto Flats, Alaska in 2002 and 2003. The estimates are predicted by the model: DSR = Year + Brood Age + Body Condition, with brood age from 1-30 days and mean female condition. Dashed lines are 95% confidence limits.

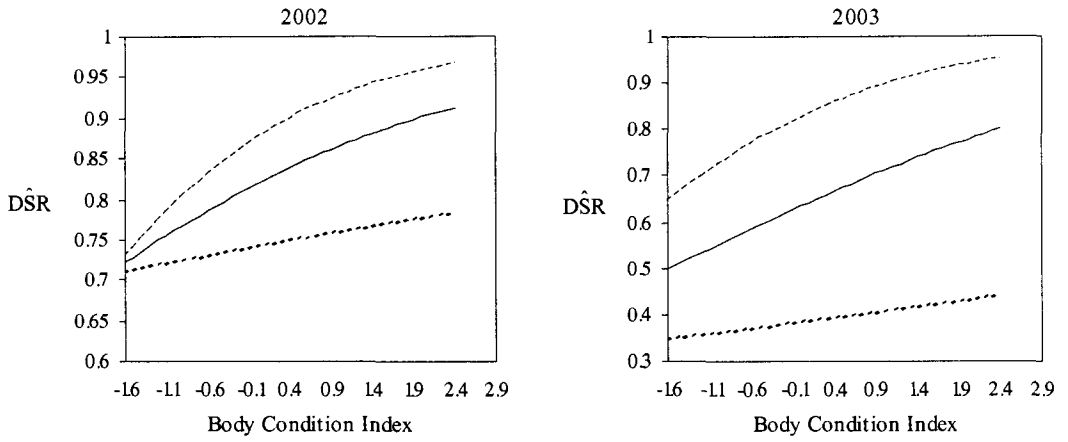

Figure 2 – The relationship between body condition of brood females and Daily Survival Rate (DSR) of ducklings at Minto Flats, Alaska in 2002 and 2003. The estimates are predicted by the model: DSR = Year + Brood Age +Body Condition, with the observed range of female condition index values and duckling age held constant. Dashed lines are 95% confidence limits.

CONCLUSIONS

The patterns of variation in nest survival of ducks at Minto Flats were inconsistent with past predictions about potential duck production in the boreal forest (Calverly and Boag 1977, Johnson and Grier 1988). During this study, the average annual rate of nest survival for all species, 0.11 (95% CI: 0.05 to 0.22) was comparable to average nest survival rates from studies conducted in the mid-continent (Higgins et al. 1992, Greenwood et al. 1995, Reynolds et al. 2001) and process variation in nest survival among years (Range: 0.02 to 0.46) was similar to estimates of spatio-temporal process variation in nest survival of the mid-continent mallard population (Range: 0.00 to 0.31; Hoekman et al. 2002). Nest survival of scaup at my study area varied from 0.01 (SE = 0.01) in 1992 to 0.61 (SE = 0.06) in 1993. Daily nest survival of all duck species was higher on islands and in forested sites than in meadows and increased with date in 1993 and 2002. The prevailing apparent cause of nest failure at Minto Flats was predation, although flooding probably caused many nest failures in 1991 and 1992 (Chapter 1). Predation has also been the leading reported cause of nest failure in the mid-continent (Sargeant and Raveling 1992).

Predation, cold temperatures, and rain have been the most common causes of duckling mortality in studies of marked ducklings throughout North America (Johnson et al. 1992, Korschgen et al. 1998, Pietz et al. 2003). During this study, duckling survival to 30 days varied from 0.23 (SE = 0.05) in 2002 to 0.03 (SE = 0.04) in 2003. Daily survival rate of ducklings increased with age, and with body condition of the brood female. I

observed little support for relationships between duckling survival and date, daily precipitation, and daily minimum temperature—or their interactions with other predictors. Ducklings attended by females in better physical condition could have had a reduced risk of predation because these females might have spent less time feeding and therefore been more attentive to their broods (Talent et al. 1983, Afton 1984, Yerkes 2000). The positive effect of duckling age could be attributed to reduced vulnerability to predation, or reduced vulnerability to exposure; however, interactions between duckling age and minimum temperature or daily precipitation were not supported. Therefore, I concluded that predation could have been the source of most duckling mortality during my study.

Mid-continent studies have often revealed strong relationships between date, weather conditions, and duckling survival (Johnson et al. 1992, Guyn and Clark 1999). Date effects are often attributed to a seasonal decline in the availability of wetland habitat for brood rearing (Johnson et al 1992, Pietz et al. 2003); however, at Minto Flats, wetlands are permanent or semi-permanent (Jacobs 1992), and predator communities are more diverse than in the mid-continent. Species of potential duckling predators at Minto Flats included red fox, mink, mew gulls, herring gulls, and northern pike (Petrula 1994, Kessel et al. 2002). In mid-continent studies, the most common predators of ducklings are red fox and mink; gulls are less common on these study areas, and weather effects on duckling survival have frequently been observed (Johnson et al. 1992, Korschgen et al 1998, Pietz et al. 2003). Because of the diversity of predators, scaup at Minto Flats

might have experienced rates of predation high enough to overwhelm the predicted effect of weather on duckling survival.

Estimated recruitment of female scaup to 30 days of age (clutch size * nest survival * duckling survival * 0.5) was 0.30 (SE = 0.19) in 2002 and 0.01 (SE = 0.01) in 2003. These estimates represent an upper bound on recruitment because they did not account for the proportion of females that failed to nest, renest, or survive the breeding season. They also did not account for the proportion of eggs that failed to hatch. Nevertheless, they further illustrated the high degree of variability in annual production of scaup at a site in the western boreal forest (Petrula 1994, Fournier and Hines 2001).

Nest survival and duckling survival are generally the most variable components of recruitment of mid-continent mallards; these parameters therefore tend to have strong influence, retrospectively, on production in these populations (Johnson et al. 1992, Hoekman et al. 2002). Variation in recruitment has been influential to the population dynamics of lesser scaup and canvasbacks as well (Anderson et al. 1997, Anderson et al. 2001, Koons 2001, Brook 2002). Recruitment in mid-continent duck populations is thought to be highly variable in space and time and strongly related to variation in predation risk (Johnson et al 1992, Sargeant and Raveling 1992). Knowledge of variation in recruitment parameters among populations of ducks breeding in the boreal forest is relatively limited, however. Therefore, most predictions about duck production in the boreal forest have been predicated on differences in the stability of wetland habitat and predator communities between the boreal forest and the mid-continent and the energetic

cost of longer migrations (Calverly and Boag 1977, Johnson and Grier 1988). Contrary to these predictions (i.e., that duck production in the boreal forest is generally lower and less variable than in the mid-continent) my study indicated that both nest survival and duckling survival have been highly variable among years at Minto Flats. Studies of scaup production conducted at Minto Flats and other sites in the boreal forest have indicated that recruitment in the boreal forest was similar to the mid-continent in terms of average clutch size and nest survival rate and, furthermore, that predation was the primary cause of nest failure (Petrula 1994, Grand 1995, Fournier and Hines 2001). Thus, although the breeding season is generally shorter in the boreal forest, potential production of ducks is probably more similar between these regions than previously thought, and occasional years of high production are probably important for the long-term persistence of populations of ducks in the boreal forest as well.

The results of my investigation of nest and duckling survival were to some extent consistent with the hypothesis that reduced recruitment may be related to declines in abundance of scaup in interior Alaska (Hodges et al. 1996) and across North America (Afton and Anderson 2001). Nonetheless, my two-year study at one site in the boreal forest could not address the spatial variation in production of scaup that is evident from the pattern of declines among survey strata observed by Afton and Anderson (2001). At present, I am unaware of any existing information from concurrent studies of production of scaup across the boreal forest over multiple years; such information would provide stronger inference to the continental population dynamics of scaup. Furthermore, direct

examination of the interaction between predators and recruitment rate, possibly through experimental manipulation of predator abundance, could provide useful information about the influence of predators on recruitment of scaup.

Past management of the continental scaup population has largely consisted of alteration of hunting season lengths and bag limits under the assumption that hunting mortality is additive to natural mortality in these species (Allen et al. 1999), and there is some evidence that scaup populations may increase in response to shortened seasons and reduced bag limits (Allen et al. 1999, Afton and Anderson 2001). Recruitment is also important to scaup populations (Afton and Anderson 2001, Koons 2001, Brook 2002, this study) therefore, conservation of breeding habitat is also warranted. Because the boreal forest is currently undergoing climate change (Kroneberg and Watt 2000) and increased resource development (Zolkewich 1998), conservation of habitat in important breeding areas would probably be more important to future production of scaup (Kadlec and Smith 1992). Additionally, annual monitoring of production at several areas with high densities of breeding scaup could be useful to inform harvest management and set population goals. Because the populations of scaup have declined, and continue to decline (Wilkins and Otto 2003), and great annual variability in production appears to have been common across the boreal forest, scaup populations would probably benefit most from conservative management of harvest and direct conservation of breeding habitat.

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